

Title: Urbanization dampens the latitude-diversity cline in ants

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Abstract

1. The increase in species diversity from temperate to tropical regions is one of the most widespread patterns in biogeography. As humans continue to drastically modify natural habitats, land-use changes such as the development of cities could potentially alter typical latitudinal diversity gradients. Cities could depress or enhance biodiversity through filtering, localized extirpations, or increasing niche availability, respectively.
2. To address these possibilities and the consequences for the latitudinal diversity gradient, we constructed a global dataset of urban species diversity (richness) and community composition across ~60 degrees of absolute latitude and from 63 cities. We focused our study on ants, for which comparable urban and nonurban diversity data are broadly available.
3. We found that urbanization significantly dampened the latitude-diversity cline. The effects of urbanization varied with latitude: at lower latitudes, cities were relatively species poor and harbored distinct ant communities relative to nearby nonurban communities. In higher latitude cities, both species richness and community composition were more similar to the surrounding nonurban ant communities.
4. Our analyses suggest that the strongest impacts of urbanization on ant diversity may be in the tropics, where biological diversity is already expected to experience the greatest risk of extinction in the face of climate change.

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Introduction

One of the most frequently documented patterns in macroecology is the latitudinal diversity gradient, where species diversity decreases with increasing latitude (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003). With the emergence of global datasets, multiple studies have investigated why this relationship exists and have developed multiple hypotheses explaining this pattern, including species-energy relationships, and systematic differences in speciation and extinction rates (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003). These advances have improved our understanding of the patterns and drivers of global biodiversity. However, few studies have considered how human alterations to natural environments, such as urbanization, might modify or disrupt these well-established relationships. This is despite the recognition of the potential impact of urbanization on local-scale patterns of biodiversity (Baldock et al., 2015; Nilon, 2011; Sadler et al., 2010).

With over half of the world's population now living in cities (United Nations, 2015) and approximately 3% of the global terrestrial surface consisting of heavily altered urban land cover (Liu et al., 2014), urbanization represents a pervasive anthropogenic challenge for biodiversity. At a global scale, the processes associated with urbanization typically reduce species richness relative to the surrounding natural areas (Aronson et al., 2014; Grimm et al., 2008; Luck and Smallbone, 2010; Niemelä and Kotze, 2009; Saari et al., 2016; Wenzel et al., 2020). These losses are exacerbated by human-mediated introductions of exotic species, which often generate novel, but species-poor communities through the replacement and suppression of native species (Gippet et al., 2017; McGlynn, 1999; Sanders et al., 2003; Winter et al., 2009). Moreover, the addition of exotic species is often insufficient to recoup the loss of native species diversity in cities (Faeth et al., 2011). Coupled together, biological communities in cities often have fewer species, and/or different species, from those of the surrounding natural communities. Such urban-specific loss of native species might therefore decrease the typical latitude-diversity relationship in cities if few exotic species replace many native species (Figure 1a). Alternatively, cities might cause the typical latitude-diversity relationship to become noisier rather than systematically dampened (Figure 1b). Recent studies have challenged the universality of urban biodiversity loss by demonstrating that diversity in some cities is maintained or even increases relative to surrounding non-urban areas (Hill et al., 2017; Menke et al., 2011; Perez and Diamond, 2019; Saari et al., 2016). If cities harbor idiosyncratic gains and losses of biodiversity, the latitude-diversity relationship might therefore simply become noisier, depending on the magnitude of the urban-nonurban diversity change relative to the latitudinal signal.

Another important consideration for the impact of urbanization on the latitude-diversity relationship is whether the effects of urbanization on biodiversity themselves systematically vary

with latitude (Figure 1c). For example, a latitudinal cline in the effects of cities on biodiversity could be driven by shifts in the costs and benefits of urban warming across latitude. Urban heat island effects are a consistent feature of cities across latitude (Oke, 1982), however, urban heat islands could be expected to have benign consequences on biodiversity at higher latitudes, but detrimental consequences at lower latitudes. As ectothermic species tend to be thermally limited by cold temperatures at high latitudes, cities could relax this constraint where background temperatures are cooler. By contrast, ectothermic species tend to be near their limits of thermal performance at low latitude, in which case, cities could induce thermal stress in these warmer background temperature environments (Deutsch et al., 2008; Ghalambor et al., 2006; Tewksbury et al., 2008). Thus, rates of species loss in cities could be disproportionately high in the tropics. Although data are currently sparse, some studies are suggestive of urban diversity preservation at higher latitudes and loss at lower latitudes (Youngsteadt et al., 2017). Such a pattern could create a dampening effect on the latitude-diversity cline, with the effects of urbanization varying with latitude (Figure 1c).

We compiled a dataset of species richness and community composition of ants in cities and adjacent non-urban areas to examine the impacts of urbanization on the latitude-diversity gradient. We focused on ants, as they are ubiquitous in nearly every terrestrial ecosystem, including cities, and patterns of global ant diversity closely follow patterns of other taxa (Dunn et al., 2010; Economo et al., 2018; Kaspari et al., 2003; Kusnezov, 1957; Lach et al., 2010; Moreau and Bell, 2013; Santos, 2016). Furthermore, ants already exhibit a strong latitude-diversity relationship, making them an excellent candidate system to explore the impacts of urbanization on latitudinal clines in diversity (Kusnezov, 1957). Finally, ant diversity is highly responsive to biogeographic variation in climate including temperature and precipitation, as well as to variation in habitat disturbance (Gibb et al., 2015). Using a paired study design wherein we calculated the species richness of individual cities and nearby nonurban communities, we tested whether cities dampened the latitude-diversity gradient, that is, whether ant species richness in cities was reduced relative to that in surrounding areas. We then explored the basis for our observed patterns, specifically by asking: 1) whether urbanization tends to reduce diversity, 2) whether urban community composition differs from the nearby nonurban community, and 3) whether impacts of urbanization on diversity and composition vary across latitude.

Materials and Methods

Developing the ant species richness and community composition database

We developed a global ant species richness dataset derived from studies conducted in both urban and nonurban areas (hereafter referred to as habitat). To develop the urban data subset, we consolidated georeferenced data of species richness and community composition by searching Google Scholar and Web of Science using the following keywords: urban, ants, community,

richness, and diversity (last accessed date: Nov 6, 2019). From this search, we found 35 studies (63 cities) that reported species richness in urbanized environments (Figure 2, Supplementary Table 1). We defined urban environments as sites located within city boundaries, outdoors and embedded within urban development; no samples from within buildings were included. These studies followed standard ant survey protocols such as pitfall trapping, timed hand sampling, baiting, and litter extractions (Bestelmeyer, 2000). Due to the limited number of studies investigating ant species richness in cities, our analyses used raw values of species richness as opposed to rarified values. Sampling method and effort varied among studies, and few studies reported a measure of species abundance. As a result, we were unable to effectively subset the data by sampling method or reported metrics, however this potential confounding effect was controlled for in our analyses by including study ID as a model term (Pautasso et al., 2011).

Next, we gathered nonurban ant species richness data, using the Global Ants Database (GLAD, Gibb et al., 2017). We selected nonurban studies by identifying georeferenced GLAD records within the region of each city (250 km radius buffer around each city with urban species richness data). Owing to the large amount of interspecific variation in flight dispersal distances (four orders of magnitude Helms, 2017), we selected this radius as it would reasonably separate regional scale species pools, i.e. the radius is over 30 times the mean of known ant flight distances (Helms, 2017). We found 50 studies (57 sites) that met this criterion (Figure 2, Supplementary Table 1).

Lastly, we used a combined dataset across the 35 urban and 50 nonurban studies to explore differences in community composition. To develop the urban data subset, we identified urban studies that minimally identified morphospecies within genera, sampled within a focal city. To develop the nonurban data subset, we identified regional nonurban studies (within a 250km radius around each city) that similarly reported at least morphospecies within genera. This resulted in 30 pairs of urban and nonurban (morpho-)species lists, each pair matched by city.

Controlling for intercity variation in the degree of urbanization

As the degree of urbanization could potentially influence absolute differences in ant species richness among cities and relative differences in community composition between urban and nonurban paired sites, we quantified the degree of urbanization for the region of each city in our study. We estimated the mean percent-developed impervious surface area (ISA) of a 250 km buffer, using data derived from the global density of constructed ISA data set (Elvidge et al., 2007). ISA is the percentage of surface area covered by artificial surfaces such as concrete, with larger percentages indicating increased urban development. Mean ISA was calculated using the *zonal statistics* tool in ArcGIS v10.4.

Statistical analyses

The effect of urbanization on the latitude-diversity cline

To examine the impacts of urbanization on the latitude-diversity cline in ants, we constructed a series of linear mixed-effects models with the main effects and interaction effects of habitat (urban and nonurban) and latitude (absolute latitude). In some cases, multiple reports of species richness originated from the same study (54/120 observations, 15/81 studies), therefore we modeled “study ID” as a random effect to account for the non-independence of values from the same study. This model allowed us to evaluate several hypotheses and predictions: 1) urban dampening of the latitude-diversity cline would be indicated by a significant habitat \times absolute latitude interaction term with the slope for the urban habitat being smaller than the nonurban habitat; this outcome agrees with our *a priori* prediction; 2) conversely, a significant habitat \times absolute latitude interaction term with the slope for the urban habitat being greater than the nonurban habitat would indicate urban enhancement of the latitude-diversity cline; this outcome is against our *a priori* prediction, but plausible if cities have marginal reductions in biodiversity at low latitudes and more substantial species losses at high latitudes; 3) a non-significant habitat \times absolute latitude interaction term would indicate similar latitude-diversity clines across urban and nonurban habitats, assuming the latitude main effect is still significant to demonstrate the presence of the already well-established latitude-diversity cline in ants from unaltered habitats; although this outcome is against our *a priori* prediction, it is nonetheless plausible if cities only have marginal impacts on biodiversity; and 4) a non-significant habitat \times absolute latitude interaction term but with significant main effects of absolute latitude and habitat type, particularly in which the urban mean biodiversity is lower than non-urban, would indicate that cities reduce biodiversity, but do so similarly across latitude, *i.e.* that cities proportionally reduce biodiversity relative to the nonurban species pool; this outcome is against our *a priori* prediction, but plausible if latitude is the primary filter on diversity, with city effects on diversity acting secondarily and in proportion to regional species pool diversity.

In the event of a significant interaction between habitat and absolute latitude, we further used this as justification to quantify the latitudinal cline for each habitat type separately. To accomplish this, we performed separate linear mixed effect models for each habitat type, urban and nonurban. Finally, we quantified the degree to which the urbanization effect alters estimates of the latitude-diversity relationship, by constructing a linear mixed-effect model pooled across habitat type, with the main effects of absolute latitude, and the random effect of “study ID”. We then compared model coefficients from the habitat-pooled model to the separate nonurban only model. All analyses of species richness were performed using the *nlme* package (Pinheiro et al., 2017) in R (R Core Team, 2018).

The effect of urbanization on community composition

After exploring the effects of urbanization on the latitude-diversity cline, we explored changes in community composition. We used permutational multivariate analysis of variance (PERMANOVA) based on genus occurrence and using Sørensen (which is appropriate for occurrence based data) dissimilarity matrices. Species level data was not available for all studies included in the analysis, however genus and species diversity have been found to be highly correlated when describing biodiversity patterns in ants. We included habitat type (urban and nonurban), absolute latitude and their interaction as predictors. We performed 999 permutations for each test (McArdle and Anderson, 2001). With this analysis we were able to specifically ask whether cities harbored unique ant communities or whether they had similar community composition as nearby nonurban areas (as assessed with the significance of the habitat type term), and whether these trends depended on latitude (as indicated by a statistically significant interaction between habitat type and absolute latitude). To visualize shifts in community composition, we performed nonmetric multidimensional scaling (NMDS) based on a genus occurrence, Sørensen dissimilarity matrix ordinated along two dimensions. Both analyses for community composition were conducted with the *vegan* package (Oksanen et al., 2017).

Results

Urbanization dampens the latitude-diversity cline in ants

The number of ant species in non-urban communities declined as latitude increased (Table 1, Figure 3). However, and consistent with our expectation (Figure 1c), urbanization dampened, but did not eliminate, the latitude-diversity cline. Indeed, we found a significant interaction between habitat and absolute latitude ($P = < 0.001$, Table 1, Figure 3) such that the decline in diversity with increasing latitude was more steep for the nonurban habitat communities compared with the urban habitat communities (Nonurban: $\beta = -1.537$, $\chi^2 = 22.509$, $P = < 0.0001$; Urban: $\beta = -0.769$, $\chi^2 = 13.543$, $P = < 0.001$, Table 2, Figure 3). The difference in the latitudinal diversity gradient between cities and non-urban areas changed slightly when we accounted for variation among cities in their degree of urbanization (approximated by ISA). When we compared the slope estimate from the habitat-pooled model of species richness (pooled across habitat type) to that of the model with only the nonurban data, we found a difference of nearly 0.5 (Habitat-pooled model: $\beta = -1.126$, $\chi^2 = 29.028$, $P = < 0.0001$; Nonurban only model ($\beta = -1.537$, $\chi^2 = 22.509$, $P = < 0.0001$, Table 2). In other words, for every 1 degree change in absolute latitude, diversity was being underestimated by half a species in the model that ignored the effect of urbanization.

For both the species richness and community composition analyses described below, the inclusion of the magnitude of urbanization (ISA) of a given city did not qualitatively change our results (Supplementary Table 2, Supplementary Table 3). To simplify our analyses, we excluded ISA from the final models.

Community composition in urban and non-urban ant communities is similar at high latitudes, but not low latitudes

Ant community composition differed between urban and non-urban habitats, varied with absolute latitude, and depended on the interaction between habitat and latitude (Table 3), suggesting that differences between urban and nonurban composition varied geographically (Figure 4, stress = 0.1080). Specifically, at high latitudes, urban and nonurban communities were similar in composition, but tended to diverge at low latitudes to the extent that in the tropics, urban communities were unique groups of species rather than subsets of the nonurban regional species pool.

Discussion

The latitudinal-diversity gradient is one of the most widely observed, fundamental patterns in ecology (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003) While this relationship has long been a central aspect of ecological research (Hawkins, 2001), there is still a lack of consensus on the underlying mechanisms (Economio et al., 2018; Gaston, 2000; Wang et al., 2011, 2009) and even less of an understanding on how malleable this pattern may be, particularly when considering ongoing global anthropogenic change, such as invasion and urbanization (Arnan et al., 2017). Cities can radically change the landscape and local climate (Grimm et al., 2008). However, few studies to date have examined whether urbanization may alter latitudinal diversity gradients. Here, we found that urbanization dampens the latitudinal diversity gradient for ants (Figure 3), largely driven by differential urban effects across latitude, where cities at lower latitudes are relatively species poor and harbor unique collections of species that are distinct from the nearby nonurban species pool (Figure 4). In contrast, at higher latitudes, there was no difference in species richness nor composition between urban and nonurban sites. As a result, the strongest and most detrimental consequences on biodiversity were observed in cities at lower latitudes, a species group already at greatest risk of extinction in the face of ongoing climate change (Deutsch et al., 2008; Huey et al., 2009; Tewksbury et al., 2008).

Consistent with previous findings of ant species diversity change along broad latitudinal gradients (Dunn et al., 2010; Economio et al., 2018; Kaspari et al., 2003; Kusnezov, 1957; Ward, 2010), nonurban ant species richness was greatest at the lowest latitudes, and decreased at higher latitudes. However, while the same overall pattern held true for urban ant species richness, the degree of change was far less, with urban ants exhibiting a relatively flatter diversity-latitude

cline compared with that of nonurban ants. These results were further supported by our comparisons of our habitat-pooled model of species richness to the nonurban only model. Our habitat-pooled model estimated a decrease of approximately 1 species per 1-degree change in latitude, where the nonurban only model found that when only considering values originating from “natural” sites, species richness should decrease approximately 1.5 species per 1-degree increase in latitude. In other words, by ignoring the source of the species richness values, our model misestimated latitudinal species richness change by approximately 0.5 units. While this discrepancy is seemingly small, considering the compounding effect across the latitudinal range presented in this study (approximately 0 – 60 degrees of absolute latitude), urbanization may result in severely reduced biodiversity estimates across geographic space. From a practical standpoint, these results indicate that studies ignoring the source of species richness can have profound effects on estimates of global species richness change. Additionally, studies exploring natural biodiversity should be cautious of the proximity of study sites to nearby urban development. The physical footprint of cities is increasing globally, in order to accommodate a growing urban population (Liu et al., 2014; Seto et al., 2012), and as such, cities are no longer compact, and instead sprawl out, developing peri-urban and suburban areas (Batty, 2008). As a result, the ecological impacts of urbanization may extend beyond city boundaries, influencing biodiversity at regional scales, or as we found here, at global scales as well.

Interestingly, we found that the urban latitude-diversity cline was still present, if dampened. Specifically, because we did not find an invariant relationship between urban diversity and latitude, our study suggests that there is no fixed carrying capacity in cities as would be necessary to completely erase the latitude-diversity cline in ants. Our analyses of species richness and community composition lend support to both negligible or incomplete replacement of urban diversity at high latitude and higher rates of species loss in the tropics as explanations for the present, but dampened latitude-diversity cline. Indeed, our study might help to reconcile contrasting results for the impacts of urbanization on diversity: at lower latitudes, our study is consistent with research showing that biological communities within cities are often species poor and highly dissimilar to the surrounding nonurban communities (Aronson et al., 2014; Grimm et al., 2008; Luck and Smallbone, 2010; Winter et al., 2009). The magnitude of the tropical urban biodiversity loss was appreciable in our dataset: over one hundred species were lost from our lowest latitude city as compared with nearby nonurban sites. By contrast, at higher latitudes, our study is consistent with studies showing that cities can maintain or increase diversity, even among native species (Perez and Diamond, 2019; Saari et al., 2016), possibly through greater availability of limiting resources, or buffered seasonal fluctuations (Faeth et al., 2011).

When investigating shifts in community composition, we found significant effects of habitat type and latitude. While shifts in community composition, in response to urbanization, have been documented by numerous studies (Clergeau et al., 2006; Nancy B. Grimm et al., 2008; Hodges and McKinney, 2018; Knop, 2016; Kühn and Klotz, 2006; Thompson and McLachlan, 2007; Van Nuland and Whitlow, 2014) our results suggest that, like species richness, dissimilarity

between communities depends highly on latitude. At lower latitudes, we found distinct urban and nonurban ant communities. At higher latitudes, similarity increased, resulting in ant communities with broad genus overlap. When considering both our analysis of species richness differences and community composition, we found that urbanization did not have a uniform effect on diversity across latitude, and instead, had differential effects depending on geographic location. Our results suggest that the observed dampening effect of urbanization on the latitude-diversity cline is mostly driven by the fact that tropical cities become relatively more species poor than high latitude cities, and urban tropical ant communities are quite different from nearby nonurban habitats, while at higher latitude, urban and nonurban ant communities are more similar, with neutral to positive impacts on richness and composition at higher latitudes. These findings are limited due to the resolution of our community metrics (genera, as opposed to species), thus the similarities in composition between high latitude urban and nonurban sites may be a result of relatively less genera to draw from in the regional pool (Economato et al., 2018). However, as many of the species within these genera have been found to do well in urban habitats (Buczkowski et al 2012, Menke et al., 2011; Perez and Diamond, 2019), including established urban exploiters, such *Tapinoma sessile*, and species of *Tetramorium* (Menke et al., 2010, Sayler et al 2014, Buczkowski et al 2012), our analysis of community compositions may serve as an adequate proxy, although future research will benefit from species-level descriptions of diversity, quantifying species abundances, and standardizing sample efforts.

With ongoing rapid urban expansion, (Cincotta et al., 2000; Luck, 2007; Seto et al., 2012), there is a critical need to understand how typical biogeographic patterns might be impacted by or interact with urbanization. While this area of research is largely understudied, early evidence on the differential impact of urbanization across latitude has been observed in insect morphology (Beasley et al., 2018). In cicadas, nonurban populations exhibited the typical relationship of increasing body size with latitude, whereas urban populations exhibited the opposite trend. Urban populations of cicadas at higher latitudes were larger relative to their nonurban counterparts, reversing the expected body size-latitude relationship (Beasley et al., 2018). Consistent with our findings, the direction and magnitude of the urbanization effect varies geographically, with stronger detrimental effects at lower latitudes. Although more data are needed, it is possible that this interaction between urbanization and geographic position could be widespread among taxa and biological responses.

We found that urbanization alters global biodiversity patterns, but our work might also suggest important avenues of future research into the mechanisms underlying the latitude-diversity relationship. Climatic harshness of high latitude environments is one hypothesis for a mechanism underlying the latitude-diversity cline (Currie et al., 2004). Under this hypothesis, high latitude environments are species-poor due to limitations on performance and survival driven by low temperatures. In this context, cities provide a unique test of the climatic harshness hypothesis: on the cold end of the range of thermal performance, cities and their associated urban heat island effects might relax constraints imposed by low temperatures at high latitude sites, whereas on the

warm end of the range of thermal performance, cities might exacerbate costs of high temperatures leading species to overheat. This general pattern has been found to underlie differences in vulnerability of ectothermic species to global climate change. As global temperatures increase, stronger negative consequences on tropical biodiversity are expected, as many of these species currently live at the limits of their physiological tolerance (Deutsch et al., 2008; Huey et al., 2009; Sunday et al., 2014). The degree to which urban warming at high versus low latitudes explains the dampening of the latitude-diversity relationship in ants, and possibly other species, remains unclear, but nonetheless represents a directly testable hypothesis.

Unfortunately, in tropical areas, where species are at the greatest extinction risk from anthropogenic climate change (Deutsch et al., 2008; Huey et al., 2009; Tewksbury et al., 2008), urban development is accelerating in growth (Cincotta et al., 2000; Luck, 2007; Seto et al., 2012), often affecting rare and endemic species, and habitats important for ecosystem functioning (Pickett et al., 2011). This places urgency on studies examining the role of urbanization in global biodiversity and identifying the mechanisms driving latitudinal variation in the effects of urbanization. Moving forward, future investigations would benefit our understanding by identifying predictable trait responses and community assembly, to urban factors such as temperature, while simultaneously investigating these responses across broad geographic scales.

Author Contributions

All authors helped developed the study and provided feedback throughout. Abe Perez, Lacy Chick, Sean Menke, and Niklas Sundebo Meldgaard collected data. Abe Perez conducted the analyses with assistance from Sarah Diamond. Abe Perez wrote the initial version of the manuscript, with important feedback and collaboration from Sarah Diamond, Lacy Chick, Sean Menke, JP Lessard, Nathan Sanders, Israel Del Toro, and Niklas Sundebo Meldgaard.

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Conflict of Interest

The authors have no conflict of interests to declare

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Table 1: Estimates and statistical significance of the predictors habitat (urban vs. nonurban), absolute latitude and their interaction on ant species richness from a linear mixed-effects model. Estimates show differences from nonurban habitats. Significance was assessed using likelihood ratio tests. Significant P -values in bold.

Term	Estimate	SE	χ^2	P
Habitat	-41.363	14.357	23.632	< 0.0001
Absolute Latitude	-1.624	0.284	33.033	0.003
Habitat \times Absolute Latitude	1.008	0.388	17.816	0.008

Table 2: Estimates and statistical significance of separate linear mixed-effects models, examining the predictor of absolute latitude on ant species richness. Models include Urban only (species richness values subsetted to those that originated from cities), Nonurban only (species richness values subsetted to those that originated from natural sites), and Habitat-pooled (both urban and nonurban species richness values are included; model does not differentiate by habitat type). Significance was assessed using likelihood ratio tests. Significant *P*-values in bold.

Model	Estimate	SE	χ^2	P
Urban only	-0.769	0.212	13.543	< 0.001
Nonurban only	-1.537	0.330	22.509	< 0.0001
Habitat-pooled	-1.126	0.211	29.028	< 0.0001

Table 3: PERMANOVA summary table examining differences in ant communities across habitat (urban, nonurban), absolute latitude, and their interaction. Significant P -values are in bold.

Term	F	R^2	P
Habitat	2.792	0.028	0.033
Absolute Latitude	35.890	0.363	0.001
Habitat \times Absolute Latitude	4.078	0.041	0.004

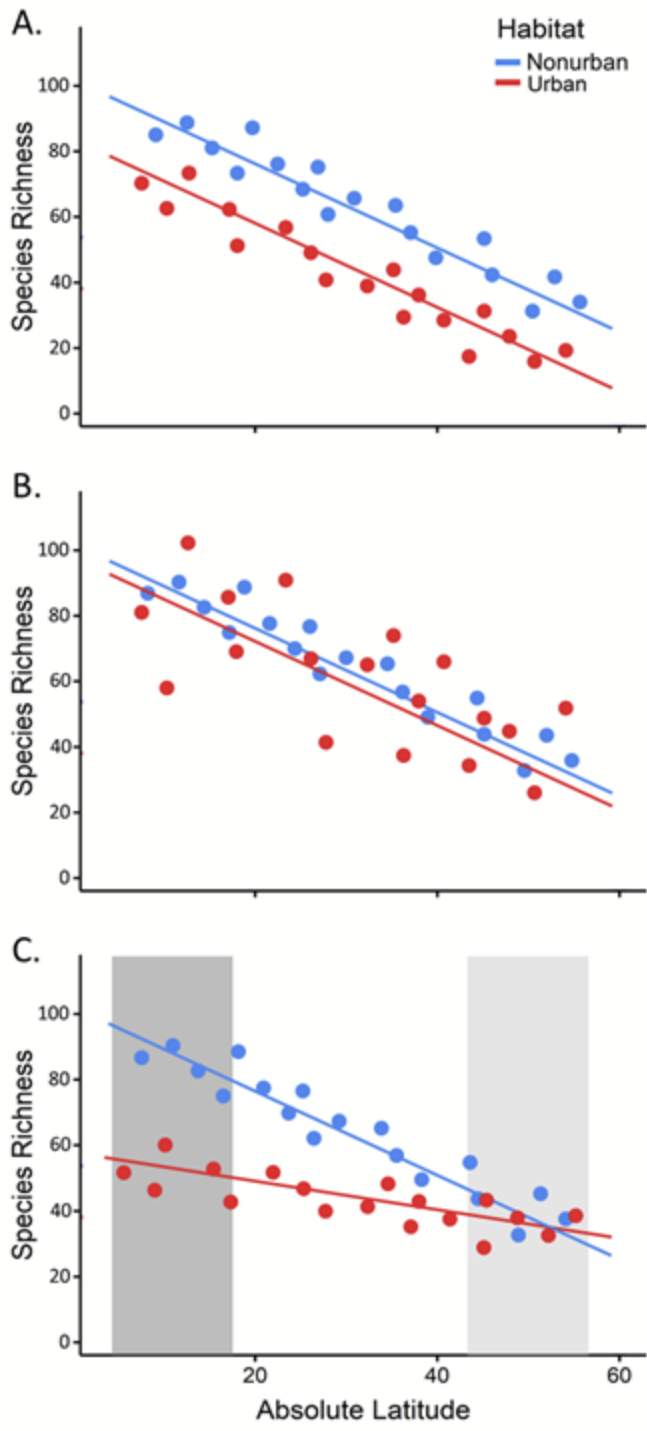


Figure 1: Three alternative hypotheses for the impacts of urbanization on the latitude-diversity cline, including (a) urban-specific loss of species diversity, (b) idiosyncratic gains and losses, and (c) differential urban impacts across latitude. (a) Consistent losses in urban species richness (red points), resulting in biological communities that are species poor relative to nonurban species richness (blue points). (b) Cities may harbor idiosyncratic gains and losses of biodiversity. Under this scenario, the broader latitude-diversity cline is maintained across cities, although noisier relative to nonurban species richness change. (c) The impact of urbanization on the latitude-diversity cline may vary with latitude. In this example, species richness loss may be disproportionately high at lower latitude cities (within dark gray box) and less so at higher latitude cities (within light gray box). Several additional alternative hypotheses are not shown: one in which cities uniformly increase diversity; one in which urban diversity is enhanced only at low latitudes; and one in which urban diversity is enhanced only at high latitudes. This is because our main hypotheses are derived from theory and empirical support, and these other alternative hypotheses are currently unsupported (though nonetheless possible), including specifically in ant systems (Gibb et al., 2015).

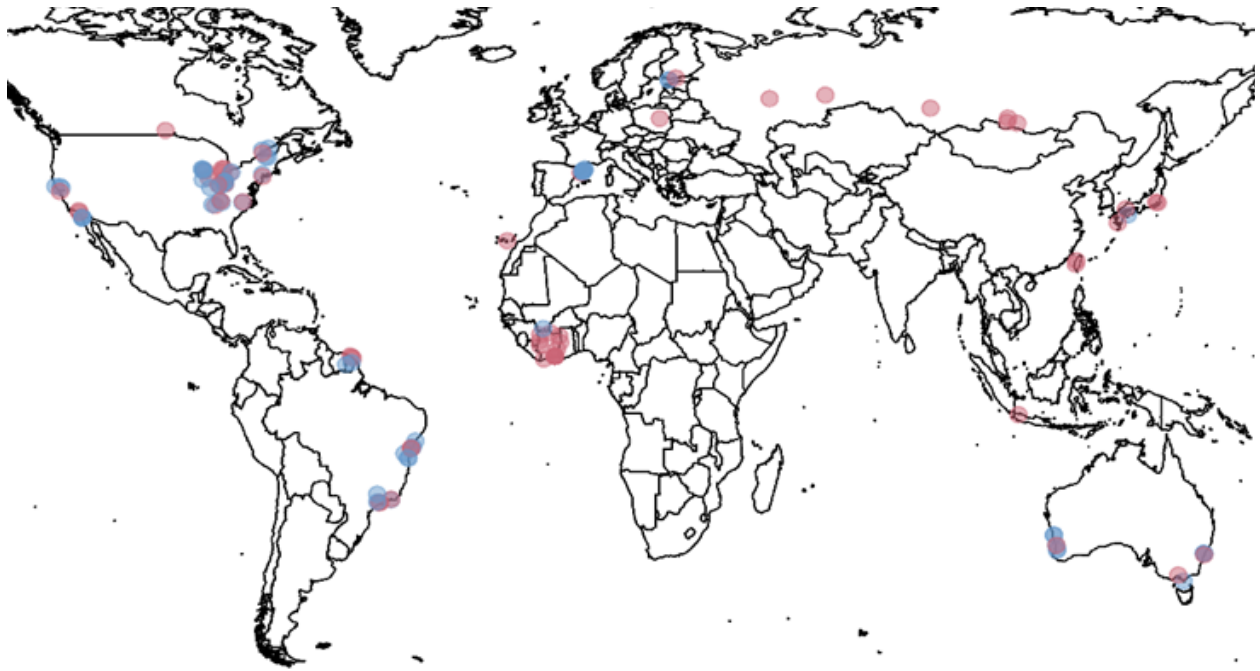


Figure 2: Geographic location of study sites used in analyses. Red points represent urban sites and blue points represent nonurban sites.

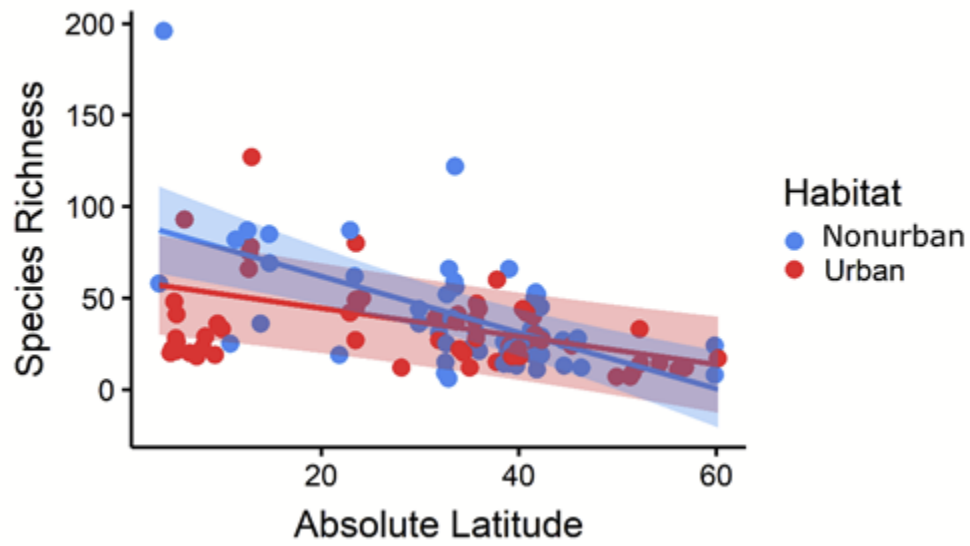


Figure 3: Relationship between species richness and absolute latitude, between urban (red points) and nonurban (blue points) habitats, with predicted values (solid lines) and 95% confidence intervals (ribbons).

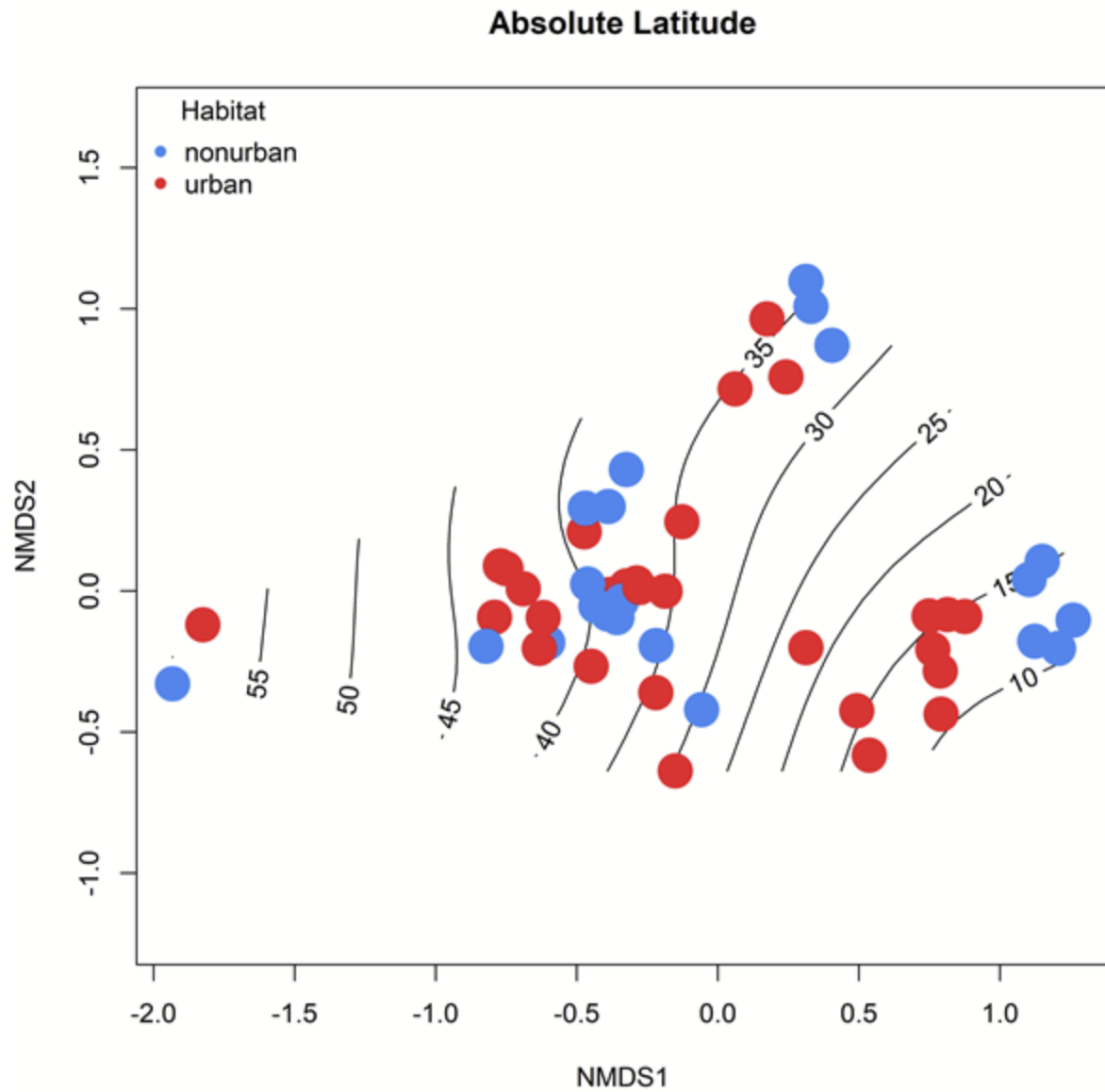


Figure 4: NMDS ordination of genus-level community composition. Each point represents the genus composition of each habitat (urban = within city, nonurban = within 250km buffer around a city). Labeled contour lines denote latitudinal trends.

Supplementary table 1. List of studies used in analyses, including habitat designation.

Source citation	Absolute Latitude	Habitat	Sampling Method
Antonov, I.A. 2008. Ant assemblages of two cities with different ecological conditions in southern Cisbaikalia. <i>Russian Journal of Ecology</i> 39(6):454-456.	51.29, 52.29	Urban	Hand Survey
Antonov, I.A. 2013. Ant assemblages (Hymenoptera: Formicidae) of cities of the temperate zone of Eurasia. <i>Russian Journal of Ecology</i> 44(6): 523-526.	51.51, 54.24, 56.11, 56.84	Urban	Hand Survey
Brooks, H. (2018). Changes in ant biodiversity across an urban gradient.	35.05	Urban	Bait
Clarke, K.M., B.L. Fisher, & G. LeBuhn. 2008. The influence of urban park characteristics on ant (Hymenoptera, Formicidae) communities. <i>Urban Ecosystems</i> 11: 317-334.	37.77	Urban	Pitfall
da Silva Melo, Tercio, et al. "Ants (Formicidae) and spiders (Araneae) listed from the metropolitan region of Salvador, Brazil." <i>Check List</i> 10.2 (2014): 355-365.	12.7, 12.77, 12.88, 12.97,	Urban	Litter Sift
Edwards, Naim. "Effects of Garden Attributes on Ant (Formicidae) Species Richness and Potential for Pest Control." <i>Urban Agriculture & Regional Food Systems</i> 1.1 (2016).	42.28	Urban	Bait, Pitfall
Espadaler, X. & L. Lopez-Soria. 1991. Rareness of certain Mediterranean ant species: fact or artifact? <i>Insect Sociaux</i> 38:365-377.	41.45	Urban	Hand Survey

Heterick, B.E., J. Casella, & J.D. Majer. 2000. Influence of Argentine and coastal brown ant (Hymenoptera: Formicidae) invasions on ant communities in Perth gardens, Western Australia. <i>Urban Ecosystems</i> 4:277-292.	31.95	Urban	Pitfall
Ivanov, K. & J. Keiper. 2010. Ant (Hymenoptera: Formicidae) diversity and community composition along sharp urban forest edges. <i>Biodiversity and Conservation</i> 19:3917-3933.	41.5	Urban	Litter Sift
Ives, Christopher D., et al. "Effect of catchment urbanization on ant diversity in remnant riparian corridors." <i>Landscape and Urban Planning</i> 110 (2013): 155-163.	33.87	Urban	Pitfall
Iwata, K., K. Eguchi, & S. Yamane. 2005. A case study on urban ant fauna of southern Kyusyu, Japan, with notes on a new monitoring protocol (Insecta, Hymenoptera, Formicidae). <i>Journal of Asia-Pacific Entomology</i> 8(3): 263-272.	31.6	Urban	Hand Survey, Bait, Litter Sift
Kouakou, L. M. M., Yeo, K., Ouattara, K., Dekoninck, W., Delsinne, T., & Konate, S. (2018). Investigating urban ant community (Hymenoptera: Formicidae) in port cities and in major towns along the border in Côte d'Ivoire: a rapid assessment to detect potential introduced invasive ant species. <i>Journal of Animal & Plant Sciences</i> , 36(1), 5793-5811.	4.74, 5.30, 5.31, 5.33, 5.35, 5.41, 6.72, 7.41, 8.04, 8.28, 9.26, 9.51, 9.97	Urban	Bait
Lessard, J.P. & C.M. Buddle. 2005. The effects of urbanization on ant assemblages (Hymenoptera: Formicidae) associated with the Molson Nature Reserve, Quebec. <i>Canadian Entomologist</i> 137: 215-225.	45.39	Urban	Pitfall

Liu, K. L., Peng, M. H., Hung, Y. C., & Neoh, K. B. (2019). Effects of park size, peri-urban forest spillover, and environmental filtering on diversity, structure, and morphology of ant assemblages in urban park. <i>Urban Ecosystems</i> , 22(4), 643-656.	24.15	Urban	Pitfall
Menke, S.B., B. Guenard, J.O. Sexton, M.D. Weiser, R.R. Dunn, J. Silverman. 2011. Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species; an example from ants. <i>Urban Ecosystems</i> 14:135-163.	35.78	Urban	Pitfall
Menke, S.B., unpublished	41.88	Urban	Pitfall
Mitrovich, Milan J., et al. "Ants as a measure of effectiveness of habitat conservation planning in southern California." <i>Conservation Biology</i> 24.5 (2010): 1239-1248.	33.68, 34.02	Urban	Pitfall
Munhae, Catarina de Bortoli, et al. "Composition of the ant fauna (Hymenoptera: Formicidae) in public squares in Southern Brazil." <i>Sociobiology</i> 53.2A and 2B (2009): 455-472.	23.52, 23.52, 23.57	Urban	Bait
Ossola, Alessandro, et al. "Urban habitat complexity affects species richness but not environmental filtering of morphologically-diverse ants." <i>PeerJ</i> 3 (2015): e1356.	37.81	Urban	Pitfall
Park, S., S. Hosoishi, & K. Ogata. 2014. Long-term impacts of Argentine ant invasion of urban parks in Hiroshima, Japan. <i>Journal of Ecology and Environment</i> 37(3): 123-129.	34.39	Urban	Hand Survey

Perez, A., & Diamond, S. E. (2019). Idiosyncrasies in cities: evaluating patterns and drivers of ant biodiversity along urbanization gradients. <i>Journal of Urban Ecology</i> , 5(1), juz017.	39.1	Urban	Pitfall, Litter Sift
Reyes-Lopez, J. & S. Carpintero. 2014. Comparison of the exotic and native ant communities (Hymenoptera: Formicidae) in urban green areas at inland, coastal and insular sites in Spain. <i>European Journal of Entomology</i> 111(3): 421-428.	28.12	Urban	Pitfall
Rizali, A., M.M. Bos, D. Duchori, S. Yamane, C.H. Schulze. 2008. Ants in tropical urban habitats: the myrmecofauna in a densely populated are of Bogor, West Java, Indonesia. <i>Journal of Biosciences</i> 15(2): 77-84.	6.18	Urban	Bait
Salyer A., G.W. Bennett, & G.A. Buczkowski. 2014. Odorous house ants (<i>Tapinoma sessile</i>) as back-seat drivers of localized ant decline in urban habitats. <i>PLoS One</i> 9(12): e113878.	40.43	Urban	Hand Survey
Santos, M. N., Delabie, J. H., & Queiroz, J. M. (2019). Biodiversity conservation in urban parks: a study of ground-dwelling ants (Hymenoptera: Formicidae) in Rio de Janeiro City. <i>Urban Ecosystems</i> , 22(5), 927-942.	22.91	Urban	Bait
Savage, Amy M., et al. "Fine-scale heterogeneity across Manhattan's urban habitat mosaic is associated with variation in ant composition and richness." <i>Insect Conservation and Diversity</i> 8.3 (2015): 216-228.	40.78	Urban	Hand Survey, Litter Sift

Lu, S. S., Huang, S. H., Bordbar, L., & Sung, I. H. (2019). Composition and diversity of ground-dwelling arthropods at Chiayi Agricultural long-term ecological research site in the Southern Taiwan. <i>Journal of Asia-Pacific Biodiversity</i> , 12(4), 561-569.	23.49	Urban	Pitfall
Slipinski, Piotr, Michal Zmihorski, and Wojciech Czechowski. "Species diversity and nestedness of ant assemblages in an urban environment." <i>European Journal of Entomology</i> 109.2 (2012): 197. - Antonov, I.A. 2013. Ant assemblages (Hymenoptera: Formicidae) of cities of the temperate zone of Eurasia. <i>Russian Journal of Ecology</i> 44(6): 523-526.	52.23	Urban	Pitfall
Tagwireyi, P., & Sullivan, S. M. P. (2016). Riverine landscape patches influence trophic dynamics of riparian ants. <i>River research and applications</i> , 32(8), 1721-1729.	39.3, 39.96, 40.10	Urban	Hand Survey
Talaga, S., Delabie, J. H., Dézerald, O., Salas-Lopez, A., Petitclerc, F., Leroy, C., ... & Dejean, A. (2015). A bromeliad species reveals invasive ant presence in urban areas of French Guiana. <i>Ecological Indicators</i> , 58, 1-7.	4.92, 5.16, 5.37	Urban	Bait
Thompson, B. & McLachlan, S. 2007. The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. <i>Urban Ecosystems</i> 10: 43-52.	49.9	Urban	Pitfall
Toennisson, T. A., Influences on the structure of suburban ant (Hymenoptera: Formicidae) communities and the abundance of <i>Tapinoma sessile</i> ." <i>Environmental entomology</i> 40.6 (2011): 1397-1404.	35.96	Urban	Pitfall

Uno, S. Cotton, J., Philpott, S. 2010. Diversity, abundance, and species composition of ants in urban green spaces. <i>Urban Ecosystems</i> 13(4): 425-441.	41.66, 42.33	Urban	Bait
Vepsäläinen, K., Ikonen, H., & Koivula, M. J. (2008, April). The structure of ant assemblages in an urban area of Helsinki, southern Finland. In <i>Annales Zoologici Fennici</i> (Vol. 45, No. 2, pp. 109-127). Finnish Zoological and Botanical Publishing Board.	60.16	Urban	Hand Survey
Yamaguchi, T. 2004. Influence of urbanization on ant distribution in parks of Tokyo and Chiba City, Japan I. Analysis of ant species richness. <i>Ecological Research</i> 19: 209-216.	35.61, 35.69	Urban	Hand Survey
Andersen, A.N., (1986). Patterns of ant community organization in mesic southeastern Australia. <i>Australian Journal of Ecology</i> , 11(1), 87-97.	39.02	Nonurban	Pitfall
Arnan, X., Rodrigo, A., & Retana, J. (2006). Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. <i>Journal of Biogeography</i> , 33(7), 1246-1258.	41.73	Nonurban	Pitfall
Bisevac, L., & Majer, J. D. (1999). Comparative study of ant communities of rehabilitated mineral sand mines and heathland, Western Australia. <i>Restoration Ecology</i> , 7(2), 117-126.	29.92	Nonurban	Hand Survey, Bait, Litter Sift
Boulton, A. M., Davies, K. F., & Ward, P. S. (2005). Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: role of plants,	38.85	Nonurban	Pitfall

soil, and grazing. <i>Environmental entomology</i> , 34(1), 96-104.			
Callan, S. K., & Majer, J. D. (2009). Impacts of an incursion of African big-headed ants, <i>Pheidole megacephala</i> (Fabricius), in urban bushland in Perth, Western Australia. <i>Pacific Conservation Biology</i> , 15(2), 102-115.	31.96	Nonurban	Pitfall
Carvalho, K.S., Souza, A.L.B., Pereira, M.S., Sampaio, C.P., & Delabie, J.H.C. (2004) Comunidade de formigas epígeas no ecótono mata de cipó, domínio da mata atlântica, BA, Brasil. <i>Acta Biologica Leopoldensia</i> 26: 249-257.	13.9	Nonurban	Bait
Delabie, J.H.C., Céréghino, R., Groc, S., Dejean, A., Gibernau, M., Corbara, B., & Dejean, A. (2009) Ants as biological indicators of Wayana Amerindian land use in French Guiana. <i>Comptes Rendus Biologies</i> 332: 673-684.	3.64	Nonurban	Pitfall
Ellison, A.M., Record, S., Arguello, A., & Gotelli, N.J. (2007) Rapid Inventory of the Ant Assemblage in a Temperate Hardwood Forest: Species Composition and Assessment of Sampling Methods. <i>Environmental Entomology</i> 36(4): 766-775.	41.25	Nonurban	Bait, Litter Sift, Pitfall
Feitosa, R.S.M., & Ribeiro, A.S. (2005) Mirmecofauna (Hymenoptera, Formicidae) de serapilheira de uma área de Floresta Atlântica no Parque Estadual da Cantareira – São Paulo, Brasil. <i>Biotemas</i> 18(2): 51-71.	23.4	Nonurban	Litter Sift

Fisher, B.L. (1997) A comparison of ant assemblages (Hymenoptera, Formicidae) on serpentine and non-serpentine soils in northern California. <i>Insectes Sociaux</i> 44(1): 23-33.	38.83	Nonurban	Pitfall
Galle, L. (1991) Structure and succession of ant assemblages in a north European sand dune area. <i>Holarctic Ecology</i> 14: 31-37.	59.84	Nonurban	Bait
Gibb, H., & Hochuli, D.F. (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. <i>Biological Conservation</i> 106: 91-100.	33.62	Nonurban	Pitfall
Gibb, H., & Hochuli, D. F. (2003). Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. <i>Oikos</i> , 103: 469-478.	33.57	Nonurban	Hand Survey, Bait
Gibb, H. (2005) The effect of a dominant ant, <i>Iridomyrmex purpureus</i> , on resource use by ant assemblages depends on microhabitat and resource type. <i>Austral Ecology</i> 30: 856-867.	33.49	Nonurban	Hand Survey, Bait
Gibbs, M.M., Lambdin, P.L., Grant, J.F., & Saxton, A.M. (2003) Ground-inhabiting ants collected in a mixed hardwood southern Appalachian forest in eastern Tennessee. <i>Journal of the Tennessee Academy of Science</i> 78(2): 45-49.	36	Nonurban	Hand Survey
Gómez, C., Casellas, D., Oliveras, J., & Bas, J. M. (2003). Structure of ground-foraging ant assemblages in relation to land-use change in the northwestern Mediterranean region.	42.3	Nonurban	Pitfall

Biodiversity and Conservation, 12(10), 2135-2146.			
Gómez, C., Pons, P., & Bas, J.M. (2003) Effects of the Argentine ant <i>Linepithema humile</i> on seed dispersal and seedling emergence of <i>Rhamnus alaternus</i> . <i>Ecography</i> 26: 532-538. (Data from Aixart d'en Pi - unpublished)	41.97	Nonurban	Pitfall
Gómez, C. unpublished	41.97	Nonurban	Pitfall
Gotelli, N.J., & Ellison, A.M. (2002) Biogeography at a regional scale: determinants of ant species density in bogs and forests of New England. <i>Ecology</i> 83: 1604-1609.	44.5	Nonurban	Bait, Litter Sift
Groc, S., Orivel, J., Dejean, A., Martin, J.M., Etienne, M.P., Corbara, B., & Delabie, J.H.C. (2019) Baseline study of the leaf-litter ant fauna in a French Guianese forest. <i>Insect Conservation and Diversity</i> 2: 183-193.	4.09	Nonurban	Litter Sift
Herbers, J.M. (1989) Community structure in north temperate ants: temporal and spatial variation. <i>Oecologia</i> 81: 201-211.	44.59	Nonurban	Hand Survey
Holway, D.A. (1996) Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. <i>Oecologia</i> 116(1-2): 252-258.	38.5	Nonurban	Bait, Litter Sift
Holway, D.A., Suarez, A.V., & Case, T.J. (2002). Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. <i>Ecology</i> 83:1610-1619.	32.69	Nonurban	Bait, Litter Sift

Kaspari M.E, unpublished	38.53	Nonurban	Litter Sift
Leclerc, J., Francoeur, A., & Maire, A.(1991) Les fourmis de trois érablières de la région de TroisRivières, Québec (Formicidae, Hymenoptera). Revue d'entomologie du Québec 36: 43-49.	46.35	Nonurban	Hand Survey
Letendre, M., Francoeur, A., Beique, R., & Pilon, J. G. (1971). Inventaire des fourmis de la station de biologie de l'U-niversité de Montréal, St. Hippolyte, Québec (Hymenoptera: Formicidae). Le Naturaliste Canadien, 98, 591-606.	45.99	Nonurban	Hand Survey
Maeto, K., & Sato, S. (2004) Impacts of forestry on ant species richness and composition in warm-temperate forests of Japan. Forest Ecology and Management 187: 213-223.	33.2	Nonurban	Hand Survey
Majer, J.D., & Nichols, O.G. (1998) Long- Term Recolonization Patterns of Ants in Western Australian Rehabilitated Bauxite Mines with Reference to Their Use as Indicators of Restoration Success. Journal of Applied Ecology 35: 161-182.	33.2	Nonurban	Pitfall
Majer, J.D. (1980) A Preliminary Ecological Survey of the Wagerup Ant Fauna. Environmental Research Bulletin Number 7.	32.72	Nonurban	Pitfall
Majer, J.D. (1992) Ant Recolonization of rehabilitated bauxite mines of Poços de Caldas, Brazil. J. of Tropical Ecology 8: 97-120.	21.85	Nonurban	Hand Survey, Pitfall

Majer, J. D., Sartori, M., Stone, R., & Perriman, W. S. (1982). Recolonisation by ants and other invertebrates in rehabilitated mineral sand mines near Eneabba, Western Australia. Reclamation and Revegetation Research (Netherlands).	29.92	Nonurban	Pitfall
Majer, J.D., Delabie, J.H.C., & Mckenzie, N.L. (1997) Ant litter fauna of forest, forest edges and adjacent grassland in the Atlantic rain forest region of Bahia, Brazil. Insectes Sociaux 44: 255-266.	14.75	Nonurban	Litter Sift / Pitfall
Martelli, G.M., Ward, M.M., & Fraser, A.M. (2004) Ant Diversity Sampling on the Southern Cumberland Plateau: A Comparison of Litter Sifting and Pitfall Trappings. Southeastern Naturalist 3(1): 113-126.	35.21	Nonurban	Litter Sift / Pitfall
Menke, S.B., & Holway, D.A. (2006) Abiotic factors control invasion by Argentine ants at the community scale. Journal of Animal Ecology 75: 368-376.	32.58	Nonurban	Litter Sift / Pitfall
Menke, S.B., & Whitcraft, C. unpublished	32.56	Nonurban	Pitfall
Menke, S. B., Fisher, R. N., Jetz, W., & Holway, D. A. (2007). Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. Ecology, 88(12), 3164-3173.	32.89	Nonurban	Pitfall
Menke, S. B., Guénard, B., Sexton, J. O., Weiser, M. D., Dunn, R. R., & Silverman, J. (2011). Urban areas may serve as habitat and corridors for dry-adapted, heat tolerant species, an example from ants. Urban Ecosystems, 14(2), 135-163.	35.72	Nonurban	Pitfall

Menke, S.B., Gaulke, E., Hamel, A., & Vachter, N. (2015) The effects of restoration age and prescribed burns on grassland ant community structure. <i>Environmental Entomology</i> . DOI 10.1093/ee/nvv110	42.23	Nonurban	Pitfall
Menke, S.B., unpublished	42.24	Nonurban	Pitfall
Parr, C.L., unpublished	10.81	Nonurban	Hand Survey, Pitfall
Perez, A., & Diamond, S. E. (2019). Idiosyncrasies in cities: evaluating patterns and drivers of ant biodiversity along urbanization gradients. <i>Journal of Urban Ecology</i> , 5(1), juz017.	39.00, 39.77, 41.61	Nonurban	Litter Sift / Pitfall
Petersen, C. E., Zwolfer, K., & Frandkin, J. (1998). Ant fauna of reconstructed tallgrass prairie in northeastern Illinois. <i>Trans Ill Acad Sci</i> , 91, 85-90.	41.84	Nonurban	Pitfall
Retana, J., & Cerdá, X. (2000) Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. <i>Oecologia</i> 123: 436-444.	41.6	Nonurban	Bait, Litter Sift
Sanders, N.J., Lessard, J., Fitzpatrick, M.C., & Dunn, R.R. (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. <i>Global Ecology and Biogeography</i> 16: 640–649.	35.6	Nonurban	Litter Sift / Pitfall

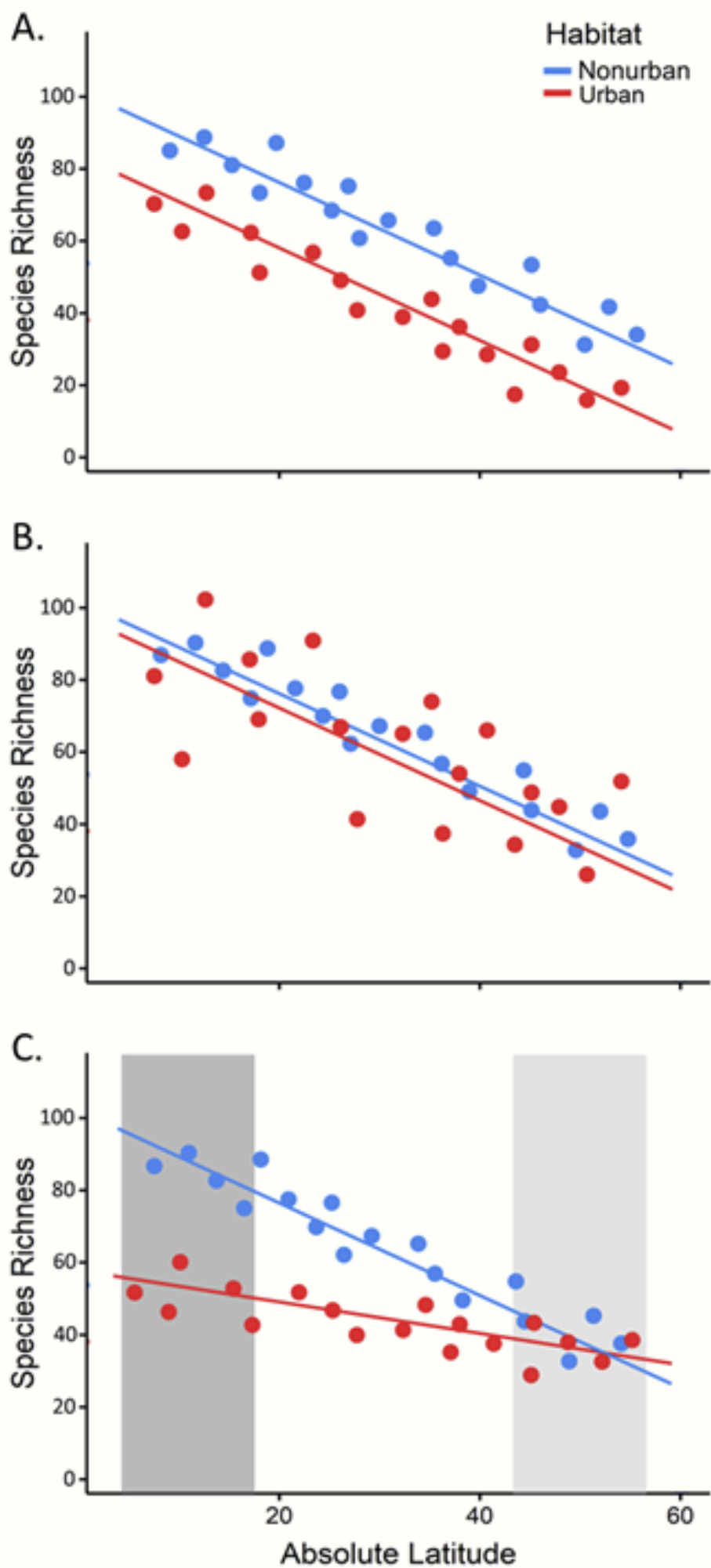
Santos, M. N., Delabie, J. H., & Queiroz, J. M. (2019). Biodiversity conservation in urban parks: a study of ground-dwelling ants (Hymenoptera: Formicidae) in Rio de Janeiro City. <i>Urban Ecosystems</i> , 22(5), 927-942.	22.96	Nonurban	Bait
Savolainen, R., & Vepsalainen, K. (1989) Niche differentiation of ant species within territories of the wood ant <i>Formica polyctena</i> . <i>OIKOS</i> 56: 3-16.	59.85	Nonurban	Bait, Litter Sift
Silva, R.R., & Brandão, C.R.F.(2014) Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. <i>PLoS ONE</i> 9(3), e93049.	11.37, 12.55, 14.78	Nonurban	Litter Sift
Suarez A.V., unpublished	40.15	Nonurban	Litter fist / Hand Survey
Suñer, D. (1991) Contribució al coneixement mirmecològic de Gavarres, Montgrí, Guillerries i la Serralada Transversal. Phd dissertation. Universitat Autònoma de Barcelona.	41.88	Nonurban	Pitfall
Tagwireyi, P., & Sullivan, S. M. P. (2016). Riverine landscape patches influence trophic dynamics of riparian ants. <i>River research and applications</i> , 32(8), 1721-1729.	39.29	Nonurban	Hand Survey
Parr, C.L. unpublished	10.81	Nonurban	Pitfall

Supplementary Table 2: Estimates and statistical significance of the predictors habitat (urban vs. nonurban), impervious surface area (ISA), absolute latitude, and their interactions on ant species richness from a linear mixed-effects model. Estimates show differences from nonurban habitats. Significance was assessed using likelihood ratio tests. Significant *P*-values in bold.

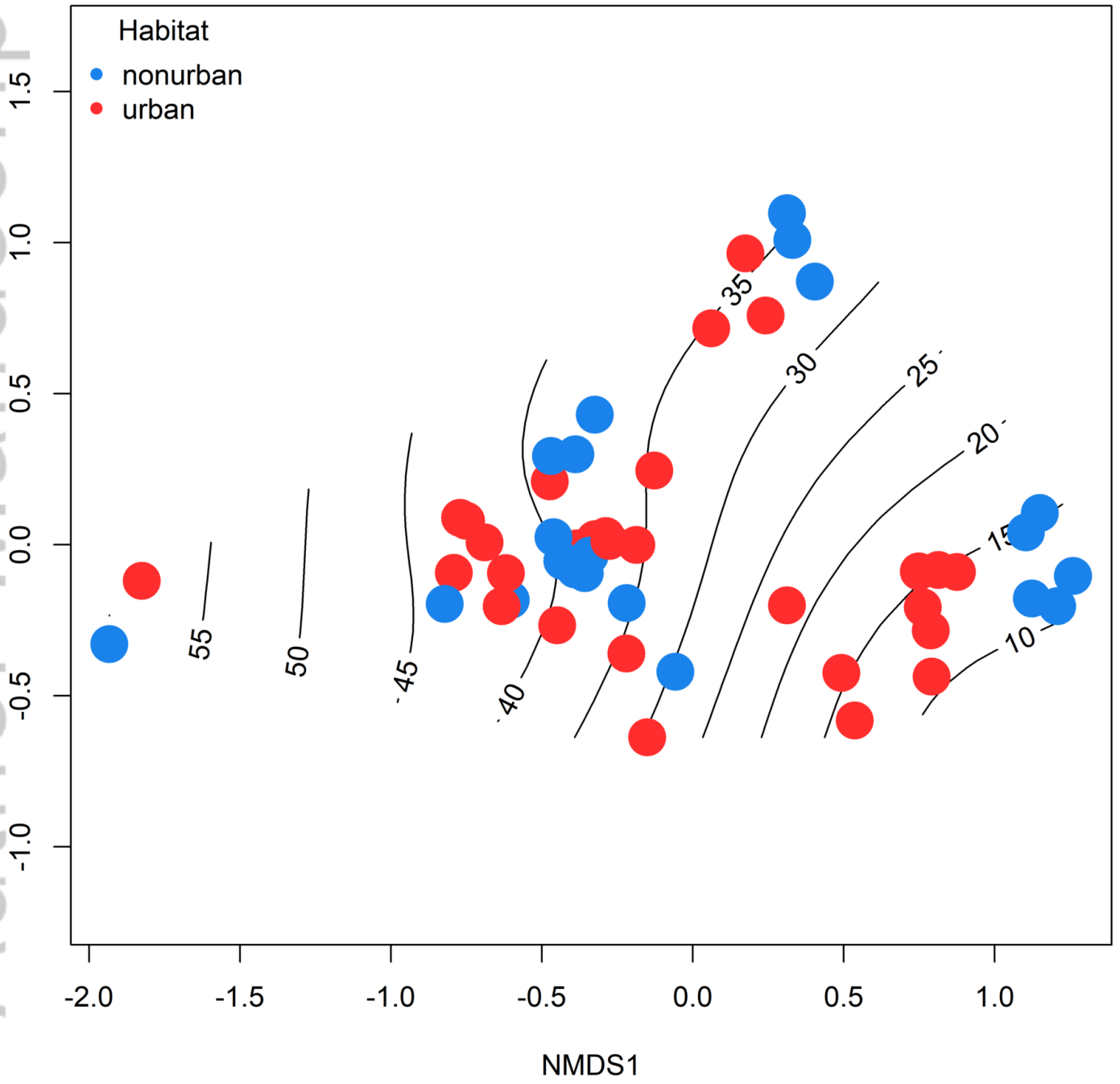
Term	Estimate	SE	χ^2	<i>P</i>
Absolute Latitude	-1.63204	0.28718	33.9962	< 0.0001
Habitat	-49.8157	15.52683	10.8354	0.001
ISA	0.17305	0.118797	2.2337	0.135
Absolute Latitude × Habitat	1.15995	0.430067	7.6575	0.006
Absolute Latitude × ISA	-0.00314	0.003151	1.0449	0.307

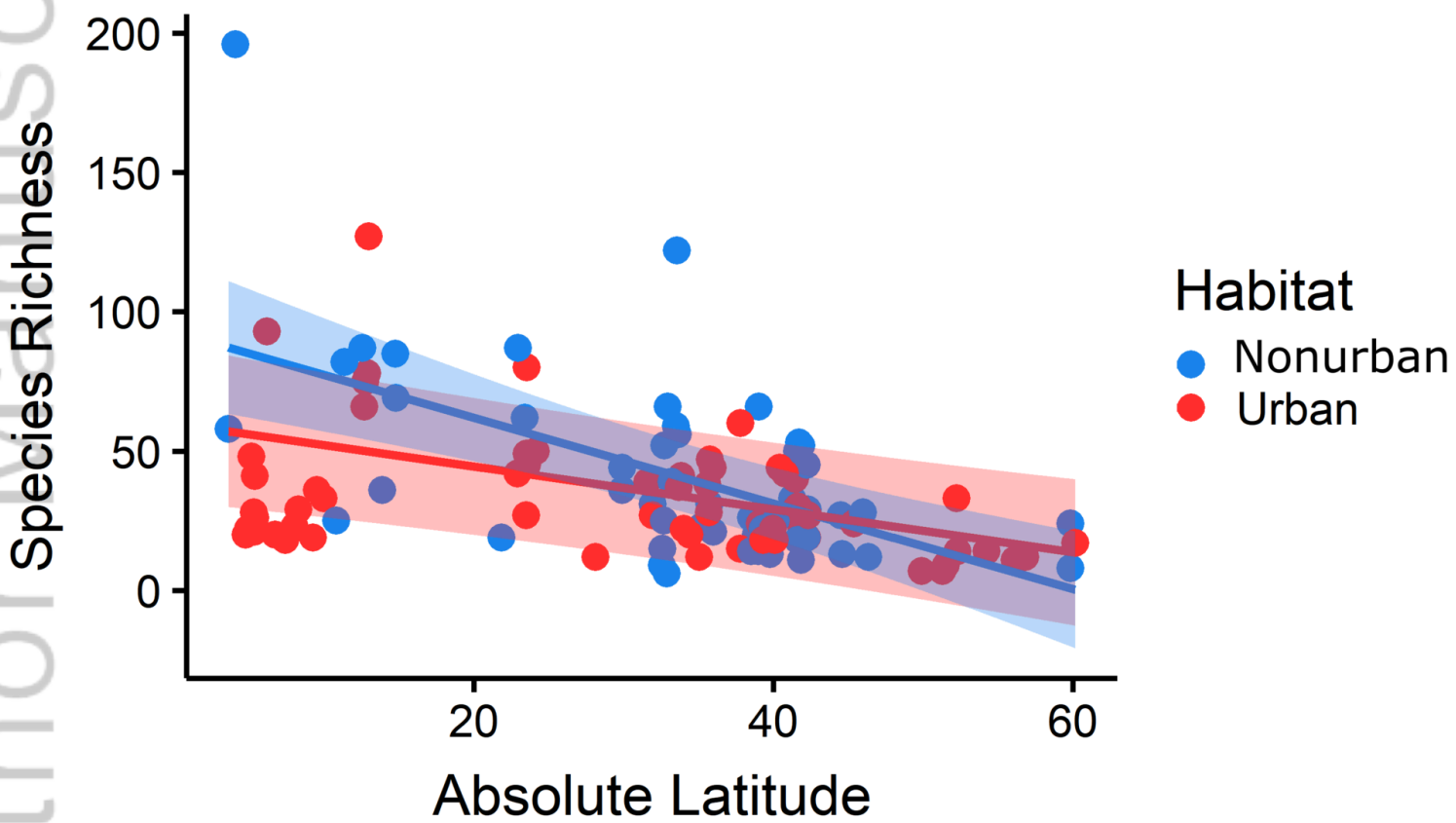
Supplementary Table 3: Estimates and statistical significance of the predictors absolute latitude and impervious surface area (ISA), from a linear regression, on species richness differences (urban minus nonurban species richness).

Term	Estimate	SE	<i>F</i>	<i>P</i>
Absolute Latitude	-0.9805	0.4824	4.1308	<i>0.051</i>
ISA	-0.1014	0.2065	10.8354	0.627

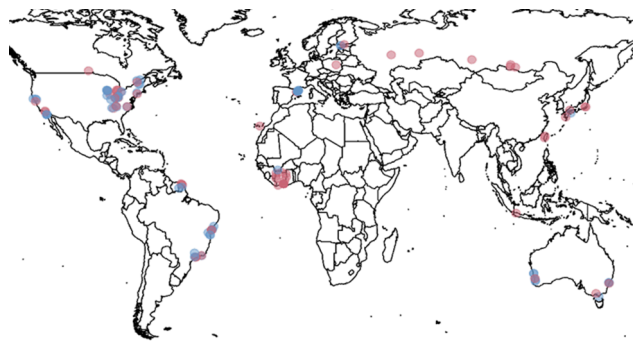


Absolute Latitude





ICAD_12598_FIG_speciesrichness_solo.tif



ICAD_12598_globe_map_3.tif

Graphical Abstract:

Title: Urbanization dampens the latitude-diversity cline in ants

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1. We constructed a global dataset of urban ant species diversity (richness) and community composition. We found that urbanization significantly dampened the latitude-diversity cline, with varying impacts across latitude.
2. Lower latitude cities were species poor with distinct ant communities relative to nearby nonurban communities. Urban and nonurban species richness and community composition were more similar at higher latitudes.
3. The strongest impacts of urbanization on ant diversity may be in the tropics, where biological diversity is expected to experience the greatest risk of extinction due to climate change.

